Catalogue of American Amphibians and Reptiles.

Whiting, M.J. and J.R. Dixon. 1996. *Phrynosoma modestum*.

Phrynosoma modestum Girard
Roundtail Horned Lizard

Phrynosoma modestum Girard, *in* Baird and Girard, 1852:69 (see Banta, 1971). Type-locality, "from the valley of the Rio Grande west of San Antonio.....and from between San Antonio and El Paso del Norte." Syntypes, National Museum of Natural History (USNM) 164 (7 specimens), subadult male, adult male, and 5 adult females, USNM 165660, an adult male, and Museum of Natural History, University of Illinois at Urbana-Champaign (UIMNH) 40746, an adult male, collected by J.H. Clark in May or June 1851 (Axtell, 1988) (not examined by authors). See Remarks.

Doliosaurus modestus: Girard, 1858:409.

A(nota). modesta: Cope, 1896:834.

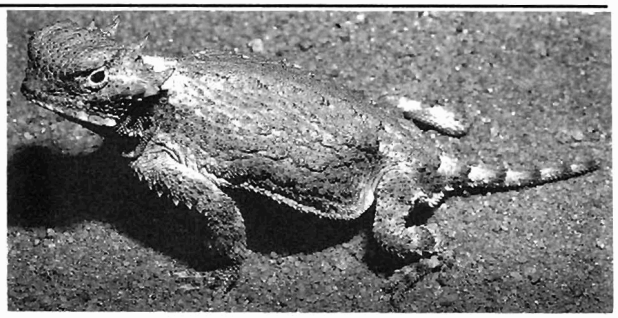
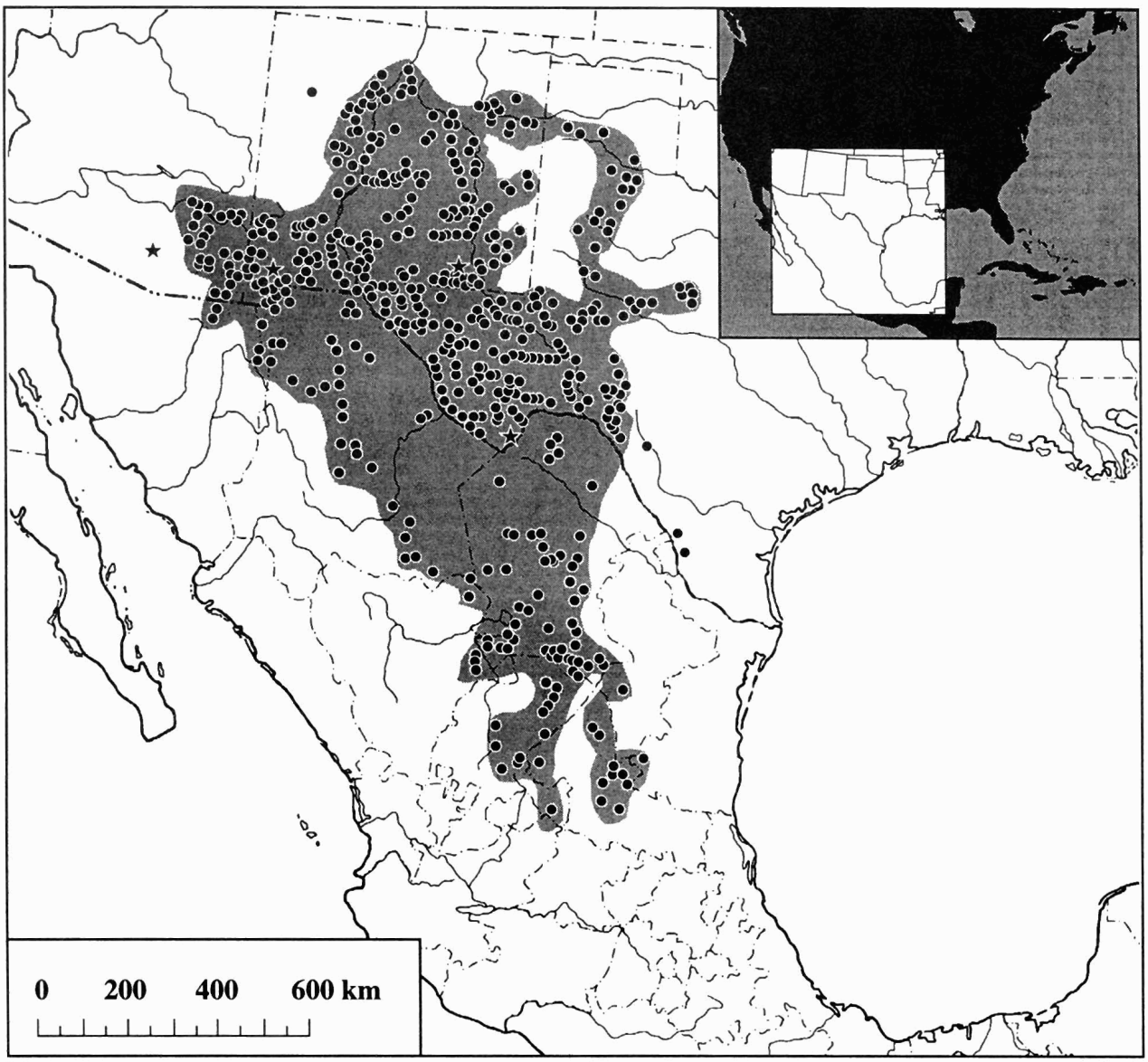


Figure. Adult *Phrynosoma modestum* from Doña Ana County, New Mexico. Photograph by Suzanne L. Collins, courtesy of The Center for North American Amphibians and Reptiles.

Phrynosoma platyrhynus: Herrick, Terry, and Herrick, 1899:136.

Phrynosoma modestrum: Morafka, Adest, Reyes, Aguirre L., and Lieberman, 1992:214. *Lapsus*.



Map. Distribution of *Phrynosoma modestum*: dots indicate specimen records, those outside of the shaded range are extralimital; the type-locality is too imprecise to plot; stars indicate fossil records.

• **Content.** No subspecies have been described.

• **Definition.** *Phrynosoma modestum* is the smallest horned lizard, with a maximum SVL of 66 mm in males and 71 mm in females (Fitch, 1981). It is the sister taxon to *P. platyrhinos*, and is part of the "northern radiation" (*sensu* Montanucci, 1987). Head length and width are approximately equal, with an abrupt rostrofrontal angle. The two temporal and two occipital spines are a distinctive feature and are of approximately equal size, although the temporals may project beyond the occipitals. The chinshields are in contact with the infralabials and decrease in size posteriorly; the penultimate chinshield is the largest. Gular scales are small and subequal; a slightly enlarged row is in contact with the chinshields. The distinctiveness of the tympanum is highly variable from complete concealment to completely exposed. Dorsal scales are small, irregular, mainly granular, and interspersed with enlarged, keeled scales (also on tail). A lateral abdominal fringe is absent, although a series of elongate spines occur on either side of the tail next to the anus. Ventral scales are relatively large and smooth. Males have 7-13 femoral pores on each leg and enlarged postanal scales. The tail is cylindrical, and narrows abruptly at the base.

The ground color varies from light gray to light brown, sometimes appearing yellowish gray. Distinctive brown blotches are on each side of the neck, and on the groin; the groin spots often extend towards the axilla. The tail is banded, and sometimes light bands are visible on the dorsum. The venter is uniform cream to white. Coloration is highly variable, but is normally population specific.

• **Diagnosis.** Chin shields in contact with infralabials, a cylindrical tail, 4 occipital spines of moderate, equal length (*Phrynosoma douglassi* has 4 short occipital spines), absence of a lateral abdominal fringe, and absence of conical, spinose dorsal scales separate *P. modestum* from all congeners.

• **Descriptions.** Comprehensive descriptions are provided by Smith (1946), Reeve (1952), and Montanucci (1987). Other descriptions include Girard (1851 [1852]), Cope (1900), Van Denburgh (1922), Cuesta Terron (1932), Smith (1934), Conant (1975), Behler and King (1979), Sherbrooke (1981), Stebbins (1954, 1985), Garrett and Barker (1987), Tanner (1987), and Conant and Collins (1991). Gorman (1973) described the karyotype (2N = 34, 12V + 22m).

• **Illustrations.** The earliest illustrations are black-and-white drawings in Girard (1851 [1852]) of the dorsum, three different aspects of the head, and an *in situ* illustration of femoral glands of a male. Line drawings of the head and a ventral view of a hind limb, reproduced from Cope (1883), appeared in Smith (1946). The horn arrangement is drawn in Conant (1975) and Conant and Collins (1991). Black-and-white illustrations appeared in Herrick et al. (1899) and Stebbins (1985). Color illustrations appeared in Conant (1975) and Conant and Collins (1991). Various skeletal elements are illustrated in Montanucci (1987). Light micrographs and transmission electron micrographs of integumental chromatophores and the dermal skin layer were given by Sherbrooke and Frost (1989). Black-and-white photographs of the skull appeared in Reeve (1952) and Olsen (1968), and a black-and-white photograph of a mandible in Montanucci (1989a). Black-and-white photographs appeared in Cuesta Terron (1932), Smith (1946), and Montanucci (1989b). Black-and-white photographs illustrating stone mimicry appeared in Sherbrooke (1981), Sherbrooke and Montanucci (1988), and Morafka and Reyes (1994). Color photographs are in Baur (1979), Switak (1979), Behler and King (1979), Sherbrooke (1981), Garrett and Barker (1987), Obst et al. (1988), and Degenhardt et al. (1996). Habitat photographs appeared in Sherbrooke (1981) and Switak (1979).

• **Distribution.** *Phrynosoma modestum* occurs in southern and western Texas, southern New Mexico, southeastern Arizona and north-central México. In México it has been recorded as far south as San Luis Potosí. Preferred habitats of this species are xeric or semixeric, including desert flats, semiarid plains and scrubland. The preferred substrate is generally rocky with an abundance of pebbles, although these lizards may be found in a variety of microhabitats that include undulating calcareous hills, talus foothills, the lower elevations of igneous mountains, sandy washes, and the flat margins of gravelly alluvial basins. *Phrynosoma modestum* is absent from the sandy zones of the Llano Estacado in northwestern Texas and eastern New Mexico, and occurs in isolated pockets of pebble soils in southern Texas.

• **Fossil Record.** Fossils are known from the Sangamon Interglacial of Cragin Quarry, Kansas (Etheridge, 1958, 1960); the middle Holocene of Deadman Cave, Arizona (Mead et al., 1984); the mid-Wisconsin Pleistocene of Dry Cave, New Mexico (Harris, 1987); the Pleistocene-Holocene of Howell's Ridge Cave, New Mexico (Van Devender and Worthington, 1977); and the Pleistocene-Holocene of Maravillas Canyon and Tunnel View (near Rio Grande Village), Texas (Van Devender and Bradley, 1994).

• **Pertinent Literature.** The taxonomic history of *Phrynosoma modestum* is discussed in detail by Reeve (1952), and the species is included in phylogenies (including biogeographic information) in Reeve (1952), Etheridge (1964), Presch (1969), Montanucci (1987), Morafka et al. (1992), and Reeder (1995). As part of their phylogenetic studies, Presch (1969), de Queiroz (1982), and Montanucci (1987) performed detailed studies of osteology. Arnold (1995) included *P. modestum* in a phylogenetic study of behavior. Range maps are in Smith (1946), Conant (1975), Behler and King (1979), Stebbins (1985), and Conant and Collins (1991); a distribution map for the United States is given in Sherbrooke (1981); regional distributions are given in Dixon (1987), Garrett and Barker (1987), Axtell (1988), Flores-Villela (1993), and Degenhardt et al. (1996). Axtell (1988) also provided a comprehensive review of the distributional records for Texas, including a discussion of problematic and erroneous records. Keys are given in Burt (1935), Reeve (1952), Smith (1946), Smith and Taylor (1950a), Dixon (1987, for Texas lizards), and Degenhardt et al. (1996, for New Mexico lizards); an illustrated key is in Sherbrooke (1981). Liner (1994) provided the Spanish common name (*Tapayatxin*).

General life history information and/or reviews are in Smith (1946), Milne and Milne (1950), Pianka and Parker (1975), and Sherbrooke (1981). An annotated bibliography with a limited number of references on *P. modestum* is in Milne and Milne (1950), and literature compendia are given by Reeve (1952), Dixon (1987), and Smith and Smith (1973, 1976, 1993). Anecdotal information is in Switak (1979). Schedules of natality and mortality are unknown for wild populations; however, Baur (1986) reported maintaining a male (initial total length = 81 mm) for five years before it was killed by a dog. Whitford and Creusere (1977) reported five years of density data for a Chihuahuan Desert population in relation to rainfall and prey availability. Density data are also available in Shenbrot et al. (1991). Body size distributions are in Barbault and Maury (1981). Degenhardt et al. (1996) presented body size data for 119 specimens from a single locality, captured over a five year period. Munger (1984b) tested whether *P. modestum* and *P. cornutum* maintain limited, non-random home ranges and if their home ranges are exclusive of one another.

Lizard community analyses which included *P. modestum* are Barbault and Grenot (1977), Whitford and Creusere (1977), Barbault et al. (1978), Barbault and Maury (1981), Creusere and Whitford (1982), Munger (1984c), and Shenbrot et al. (1991). Gehlbach (1979) studied the association between *P. modestum* and both vegetation types and other lizard species on the Guadalupe Escarpment. He also evaluated the impact of a pipeline scar on a lizard community. Other ecological notes are available for the following states: Arizona (Nickerson and Mays, 1969); Chihuahua (Dominguez et al., 1974; Tanner, 1987); Coahuila (McCoy, 1984); New Mexico (Ruthven, 1907; Little and Keller, 1937; Baltosser and Best, 1990); Texas (Jameson and Flury, 1949; Milstead et al., 1950; Minton, 1958 [1959]; Axtell, 1959; Milstead, 1959).

Lynn (1965) analysed display action patterns (head bobs) for six species of *Phrynosoma*, including *P. modestum*. Sherbrooke and Montanucci (1988) discussed horned lizard antipredatory behavior and listed all their known predators; predators of *P. modestum* were also given in Anderson and Ogilvie (1957), Reid and Fulbright (1981), and Munger (1986). Sherbrooke and Montanucci (1988) also provided correlative evidence for stone mimicry by *P. modestum*, although the hypothesis of stone mimicry remains untested. Sherbrooke (1990) documented predatory behavior of captive roadrunners (*Geococcyx californicus*) feeding on *P. modestum*, and antipredatory responses of the lizards. Sherbrooke (1987) scored behavioral responses to head immobilization in seven species of *Phrynosoma*, including *P. modestum*. In staged predatory trials between grasshopper mice (*Onychomys torridus*) and the horned lizards *P. cornutum* and *P. modestum*, Sherbrooke (1991) demonstrated a significantly higher mortality for adult *P. modestum* than for *P. cornutum*, but not between adult *P. modestum* and similar-sized juvenile *P. cornutum*. Munger (1986) reported a higher rate of death due to predation for *P. modestum* than for *P. cornutum*.

Dietary data based on stomach contents are given by Pianka and Parker (1975), and Barbault and Maury (1981). Weese (1917, 1919) reported *P. modestum* ingesting moving lead shot and sand grains. Foraging behavior of *P. modestum* and ant antipredator responses were discussed by Shaffer and Whitford (1981), and tests of optimal foraging models were given by Munger (1984a). The relationship between morphology and diet was studied by Montanucci (1989a). Aspects of the mandible and epipterygoid were correlated with the degree of myrmecophagy; *P. modestum* being among the more myrmecophagous *Phrynosoma*. Additional information on dentition is supplied by Olson et al. (1986). Schmidt et al. (1989) presented minimal data for this species on a blood-borne factor which detoxifies the venom of a staple prey of horned lizards, *Pogonomyrmex* ants. Meyer (1966) reported drinking behavior.

Anatomical aspects are discussed by Miller (1966), Presch (1970), and Lemire (1985). The presence of a parietal eye was reported by Gundy and Wurst (1976). Gular fold morphology is discussed by Montanucci (1996). Sherbrooke and Nagle (1996) included *P. modestum* in a study of mechanoreceptors in horned lizard skin. Porter et al. (1994) included this species in a study of the chromosomal location of ribosomal genes. Ectoparasites include mites (Sherbrooke, 1981); endoparasites include nematodes (Smith, 1946; Goldberg et al. 1993).

Fitch (1970) reviewed reproduction in this species. Howard (1974) presented detailed information on reproduction including size at maturity, egg development and yolk deposition, clutch size and frequency, fat body cycling, and hatchling emergence. Vitt and Congdon (1978) described body shape, reproductive effort, and relative clutch mass for three horned lizard species, including *P. modestum*. Additional reproductive data can be found in Bundy et al. (1955), Parker (1973), Pianka and Parker (1975), and Vitt (1977, 1978). Vitt and Price (1982) examined the interplay between relative clutch mass, escape tactics, and foraging mode. Baur (1979) described mating behavior in captive *P. modestum*, whereas Minton (1958 [1959]) reported on a copulation observed in the field. Observations of hatchlings are given in Smith et al. (1963) and Lewis (1950). Captive husbandry and propagation were treated by Montanucci (1989b) and Baur (1979).

Pierce (1941) studied skin color change in response to hormone injections. Sherbrooke and Frost (1989) studied integumental chromatophores and their role in color change and thermoregulation. Baur (1979) discussed coloration and causes of color change. Best et al. (1983) found melanistic individuals of *P. modestum* on the Pedro Armendariz lava field in New Mexico.

Field body temperatures are given in Heath (1965) and Pianka and Parker (1975); Heath (1965) also studied behavioral thermoregulation. Hunsaker and Johnson (1959) discussed morphological adaptations to ultraviolet light transmission. Williams (1959) reported nocturnal activity. Dawson and Poulson (1962) used this species in a comparative study of oxygen capacities of blood. Garland (1994) presented data on treadmill endurance.

• **Remarks.** Smith and Taylor (1950a, b) restricted the type-locality to Las Cruces, New Mexico, an action with which Axtell (1988) strongly disagreed (Degenhardt et al., 1986). According to Axtell (1988), the first specimen obtained was USNM 163, listed by Baird and Girard (1852) as coming from the valley of the Rio Grande west of San Antonio and now lost (Degenhardt et al., 1996). This specimen was obtained by General Churchill during the Mexican War when his army crossed the Rio Grande at Presidio del Norte (= Ojinaga, Chihuahua, México) in 1846 (Axtell, 1988). The type-series was therefore collected somewhere in west Texas.

According to Montanucci (1987), *P. modestum* and *P. platyrhinos* constitute an east-west vicariant species pair, not *P. modestum* and *P. mcallii*, as was originally suggested by Morafka (1977).

Van Devender (1980) erroneously described a fossil juvenile *P. cornutum* as *P. modestum* (T.R. Van Devender *in* Montanucci, 1987).

• **Etymology.** The name *modestum* is from the Latin *modestus*, meaning orderly, restrained, and unassuming, and presumably refers to the status of this species as the smallest member of the genus.

• **Comment.** Among horned lizards, *P. modestum* is unique as the smallest species and because of correlative evidence for stone mimicry as an antipredatory strategy against visual predators at close range (Sherbrooke and Montanucci, 1988). The strategy of stone mimicry involves an interplay between body size, shape/posture, and coloration, that has led to a set of testable predictions outlined in Sherbrooke and Montanucci (1988). Also, *P. modestum* displays high color polymorphism, although an apparent tight correlation exists between dorsal coloration and substrate color in individual populations. This, in addition to its considerable ability to change color (Sherbrooke and Frost, 1989), makes it a model organism for both field and experimental studies of natural selection.

With increasing conservation concerns for horned lizards, fundamental data on the life history and ecology of *P. modestum* are needed. This species has traditionally been difficult to study because of its cryptic nature and small size, but the advent of microtransmitters can help circumvent this (see papers by Munger). Growth rates, age/size at maturity, population structure, and survival are still unknown for this species. Also criti-

cal for conservation is some knowledge of genetic variation within and between populations.

• **Acknowledgment.** Steven D. Sroka and John Werner kindly examined the UIMNH syntype at our request.

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